THE REINSTATEMENT OF PTILIMNIUM TEXENSE (APIACEAE) AND A NEW KEY TO THE GENUS

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ABSTRACT

Ptilimnium texense J.M. Coult. & Rose is currently treated as either a synonym of P. costatum (Elliott) Raf. or a hybrid of P. capillaceum (Michx.) Raf. and P. nuttallii (DC.) Britton. A study utilizing molecular, morphological, and ecological data was undertaken to determine its taxonomic status. Evidence is presented for the recognition of P. texense as a distinct species. Ptilimnium texense is endemic to the West Gulf Coastal Plain where it occurs in bogs, acid seeps, and wet pine savannas in east central Texas, west central Louisiana, and southern Arkansas. A key to the genus Ptilimnium Raf. is provided.

KEY WORDS: endemic, Ptilimnium costatum, West Gulf Coastal Plain

RESUMEN

Ptilimnium texense J.M. Coult. & Rose desde que fue descrita por primera vez en 1909, ha sido considerada un hibrido de P. capillaceum y P. nuttallii o un sinónimo de P. costatum. Se realizó un estudio utilizando datos moleculares y morfológicos para determinar su status taxonómico. Se presentan pruebas para el restablecimiento de P. texense como especie. Ptilimnium texense J.M. Coult. & Rose es endémica de la Llanura Costera del Golfo Oeste donde se encuentra en turberas, manantiales ácidos, y sabanas húmedas de pino en la parte centro-oriental de Texas, centro-oeste de Louisiana, y sureste de Arkansas. Se presenta una nueva clave para el género Ptilimnium Raf.

INTRODUCTION

Ptilimnium texense J.M. Coult. & Rose is currently most commonly treated as a synonym of *P. costatum* (Elliott) Raf., but some authors continue to recognize it as the hybrid *P. xtexense*, with the putative parents *P. capillaceum* (Michx.) Raf. and *P. nuttallii* (DC.) Britton. A recent study utilizing nrDNA ITS sequences indicated that *Ptilimnium texense* was more closely related to *P. costatum* than to *P. capillaceum* or *P. nuttallii* (Feist & Downie 2008), but also brought into question the synonymy of *P. texense* and *P. costatum*. This was followed by extensive herbarium and field studies to examine the taxonomic status of *P. texense*. Combined evidence from morphology, ecology, and DNA sequences indicates that *P. texense* should be reinstated. *Ptilimnium texense* occurs in acidic habitats in the West Gulf Coastal Plain Region of east central Texas, west central Louisiana, and southern Arkansas (Fig. 1).

Taxonomic History.—In 1909 J.M. Coulter and J.N. Rose described Ptilimnium texense based on a specimen from Hockley, Texas, collected by F.W. Thurow. They noted that it combined "the cleft involucral bracts, characteristic fruit ribs, and shorter styles of P. capillaceum with the stouter habit, smaller fruit, and larger calyx teeth of P. nuttallii." In 1945, Mathias and Constance speculated that plants described as P. texense "seemed to be of hybrid origin," and listed the putative parents as P. capillaceum and P. nuttallii. Easterly (1957) was unable to find distinctive characters for P. texense and so accepted this assessment, stating that "this plant combines the fruit characteristics of P. nuttallii with the vegetative characteristics of P. capillaceum." None of these authors, however, presented evidence beyond these statements to support the hybrid status of P. texense and later Mathias and Constance relegated it to synonymy under P. costatum with no explanation (Lundell 1961). Some authors, however, have continued to recognize P. xtexense (Correll & Johnston 1970; Correll & Correll 1972; Diggs et al. 1999) and have given its distribution as eastern Texas in acid bogs and marshlands. These same authors have also continued to recognize P. costatum as occurring in Texas.

Molecular Studies.—In a study utilizing nrDNA ITS sequence data (Feist & Downie 2008), specimens

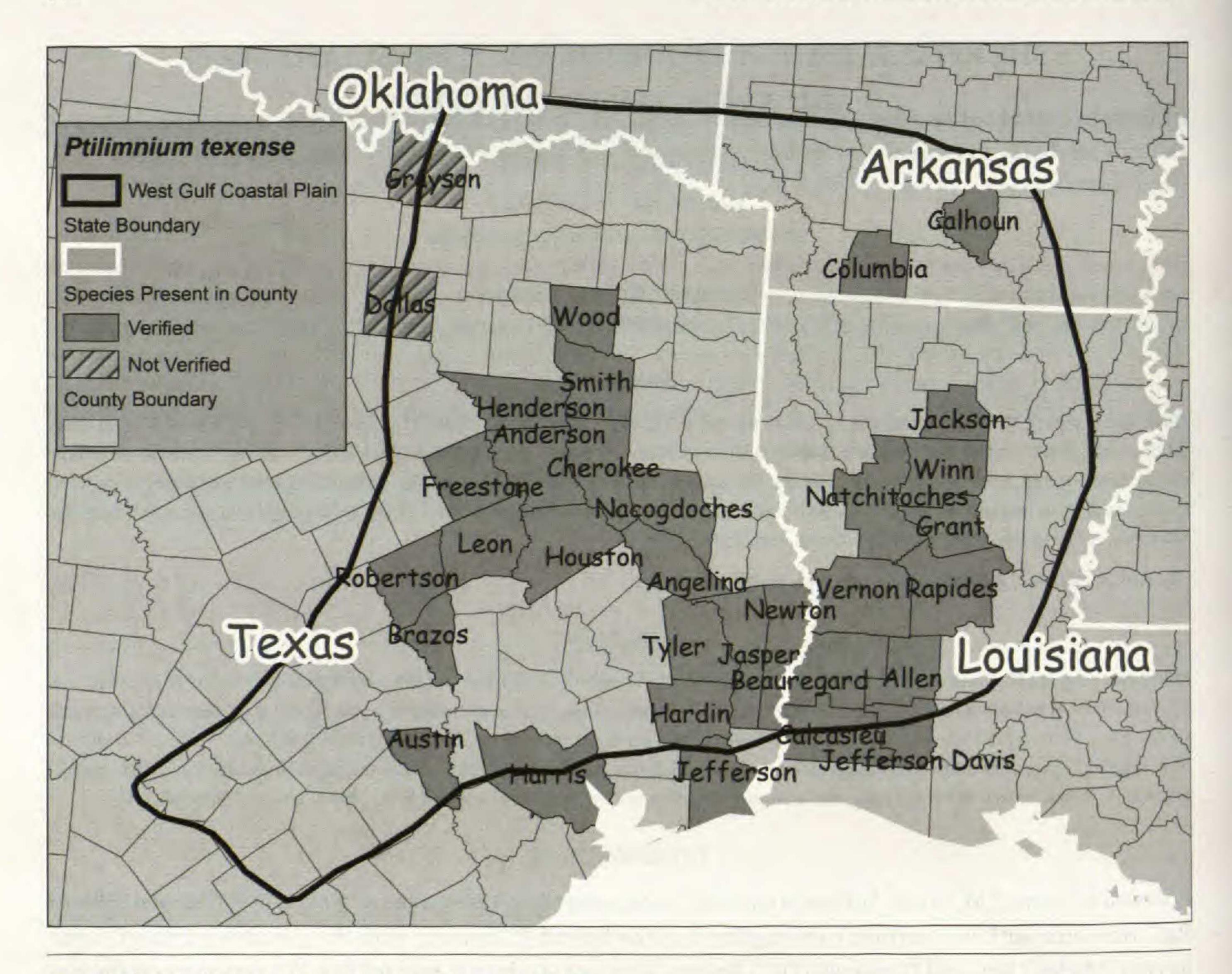


Fig. 1. Distribution of Ptilimnium texense in Arkansas, Louisiana, and Texas.

from Texas identified by Easterly as P. xtexense did not ally with either of their putative parents (P. capillaceum and P. nuttallii), but rather showed a close association with P. costatum. These specimens formed a strongly supported clade with all specimens identified as P. costatum from Texas and Louisiana (hereafter the P. texense clade). The P. texense clade was sister to another strongly supported clade made up of P. costatum from Georgia, Illinois, Missouri, and Tennessee (hereafter the P. costatum clade). These results indicated that P. xtexense was allied with P. costatum, but that populations of each from Louisiana or Texas (the P. texense clade) were molecularly distinct (Feist & Downie 2008). Average ITS sequence divergence between the P. texense and P. costatum clades was 2.6%, which is just slightly less than that between P. costatum and P. capillaceum (2.9%). Results from a recent analysis of cpDNA sequence data (trnQ-rps16 5'exon, rps16 intron, rps16 3'exon-trnK) were congruent with the ITS findings (Feist & Downie unpublished data). At first glance, these results seemed to support Mathias and Constance's conclusion (1961) that P. texense should be synonymized under P. costatum, but morphological differences between specimens making up the P. texense clade and the P. costatum clade were also observed. Taken together with the geographical and molecular differences, this suggested that members of the P. texense clade might represent a taxon distinct from P. costatum. Additional herbarium and field studies were undertaken to investigate the taxonomic status of these populations. Morphology, habit, phenology, habitat requirements, and distribution were all considered. The results of these studies are presented below.

METHODS

Field Visits and Morphological Studies.—Six populations of Ptilimnium, three in Louisiana and three in Texas, all previously identified as P. costatum but determined to be P. texense during the course of this study, were visited during Sep 15–21, 2009 (Feist & Molano-Flores specimens listed in Appendix 1). Habitat and associate species were recorded and voucher specimens were collected for additional morphological study. In addition, a total of five plants were collected live and placed in a greenhouse at the Illinois Natural History Survey.

A large number of specimens from the genus *Ptilimnium* were examined during the course of this study. Specimens were either collected by the author or borrowed from the following herbaria: ANHC, AUA, BAYLU, BRIT, DOV, DUKE, EKY, F, FLAS, FSU, GA, ILL, ILLS, JEPS, LAF, LL, LSU, LSUS, MO, NCSC, NCU, NO, NY, OKL, OKLA, OS, OSC, PH, RM, RSA-POM, SMU, TAMU, TENN, TEX, UARK, UC, UNA, UNC, US, USCH, USF, USFS, and WVA. A total of 144 specimens were determined to be *Ptilimnium texense*. These included 4 from Arkansas, 54 from Louisiana, and 86 from Texas (Appendix 1). The majority of these specimens were not identified as *P. texense* prior to this study, but were annotated to *P. texense* by the author.

Morphological data were collected from herbarium specimens. These are summarized in the taxonomic description below, and the characters critical for species identification are highlighted in the key to *Ptilimnium*. Phenology, habitat, and distribution were determined from the herbarium specimens and the accompanying label data and through field visits. Observations of root-budding (cormlet development) were made in the field and in the greenhouse.

HABITAT AND DISTRIBUTION

According to the USDA Plants Database, which treats Ptilimnium texense as a synonym of P. costatum, P. costatum occurs in 25 parishes in Louisiana and 13 counties in Texas (USDA, NRCS 2010). All specimens labeled as P. costatum examined by the author from these states are P. texense (10 parishes in Louisiana and 19 counties in Texas) or were misidentified collections of P. capillaceum or P. nuttallii. No specimens of P. costatum from Texas or Louisiana were found. Accessions of P. costatum cited from Dallas and Grayson counties (Mathias & Constance 1961; Diggs et al. 2006) could not be located. Both species grow in Arkansas but are allopatric, with P. texense occurring in two southern counties and P. costatum in three counties farther north (Fig.1).

Ptilimnium texense is endemic to the West Gulf Coastal Plain (WGCP). This physiographic region encompasses much of eastern Texas, western Louisiana, southeastern Oklahoma, and southern Arkansas (Fig. 1). Approximately 3900 species occur in the WGCP, which has been divided into four ecoregions: Oak-Pine-Hickory Forest, Longleaf-Pine Forest, Post Oak Savanna, and Prairie (MacRoberts & MacRoberts 2003). Ptilimnium texense occurs primarily in the Oak-Pine-Hickory Forest and Longleaf-Pine Forest ecoregions. The primary habitats of P. texense are bogs, acid seeps, and wet pine savannas. Common associates include Pinus palustris, Liquidambar styraciflua, Acer rubrum, Nyssa sylvatica, Magnolia virginiana, Sphagnum spp., Sarracenia alata, Oxypolis rigidior, Eryngium integrifolium, Eriocaulon spp., Osmunda regalis and O. cinnamomea. Ptilimnium texense can be added to the list of 96 species endemic to the WGCP (MacRoberts et al. 2002). About 9% of WGCP endemics are found in bogs/wet pine savannas, which occupy 10% of the total area of the WGCP (MacRoberts et al. 2002).

DISCUSSION

Ptilimnium texense was proposed as a hybrid of P. capillaceum and P. nuttallii because earlier authors felt that P. texense combined characteristics of these species and possessed no stable characters of its own (Mathias & Constance 1945; Easterly 1957). Upon closer inspection of additional specimens, unique characters that distinguish P. texense were found. Contrary to Easterly's assessment, the fruits of P. texense and P. nuttallii are easily differentiated. The fruits of P. texense are longer than those of P. nuttallii (2.2–3.5 mm versus 1–1.9 mm) and the dorsal ribs are narrow and blunt versus thick and rounded. Vegetatively, P. texense differs from P. capillaceum in that its leaf segments are always 3-4-angled to subterete and the midveins are not visible,

whereas the leaf segments of *P. capillaceum* are often flattened and the midveins are apparent. Unique characters of *P. texense* not found in *P. capillaceum* or *P. nuttallii* include root system and habit. Both *P. capillaceum* and *P. nuttallii* have fibrous roots and are annuals, whereas *P. texense* has a distinctive rounded corm at the base of the stem and is a perennial. *Ptilimnium texense* has a more limited geographic range than either *P. capillaceum* or *P. nuttallii*, and more restrictive habitat requirements, as it requires acidic environments such as bogs, acid seeps, and wet pine savannas. Where the ranges of the three species overlap, *P. capillaceum* and *P. nuttallii* flower and fruit much earlier than *P. texense*. By the time *P. texense* begins to flower in August, the fruit of *P. capillaceum* and *P. nuttallii* have already matured and fallen from the plant. The fruit of *P. texense* matures between mid-October and late November.

Molecular data provided no evidence that *P. texense* might be a hybrid. The results of studies utilizing nuclear and chloroplast DNA sequences were congruent (Feist & Downie 2008; Feist & Downie unpublished data) and there were no site polymorphisms visible on the chromatograms of accessions identified as *P. texense*. Incongruence and site polymorphisms may both be signs of hybridization (Baldwin et al. 1995; Alvarez & Wendel 2003). Taken together with the lack of morphological evidence provided by earlier authors and the distinctive characters of *P. texense* presented in this study, the hybrid status of *P. texense* is not supported.

Ptilimnium texense was synonymized under P. costatum (Mathias & Constance 1961) and it is most closely related to this species (Feist & Downie 2008). These species share some morphological traits, such as root morphology and perennial habit, but are also distinct in a number of ways (Figs. 2, 3). These differences are highlighted in the last two couplets of the key. A major difference distinguishing the species is their leaf morphology. As with P. capillaceum, leaf segments of P. costatum differ from those of P. texense by being flat with the midvein apparent. Other differences in leaf morphology include geometry and overall shape. The leaves of P. costatum are distinctive in that the primary leaf segments become progressively shorter from the leaf base to the apex and the blade apex is acute. In P. texense, the primary segments remain about the same length along the rachis and the blade apex is blunt or rounded. The leaves of P. texense are also stiffer and more three-dimensional than the leaves of P. costatum and the other Ptilimnium species. Style length also distinguishes P. texense and P. costatum. Although there can be some overlap, the styles of P. costatum are typically longer [(0.8–)1–2 mm] than those of P. texense [(0.3–)0.5–0.8(–1) mm]. There is no overlap, however, in the geographic range of these species and their habitats are different as well, with P. texense again requiring a more acidic environment. As mentioned above, both P. costatum and P. texense are perennials with corms. This structure is usually more elongate in P. costatum than in P. texense and may be slightly L-shaped. These characters have not been noted in previous studies of Ptilimnium. All species of Ptilimnium had been thought to be annuals with fibrous roots. P. costatum and P. texense do develop numerous adventitious roots which may obscure the corm, but both species develop buds from the corm (cormlets) that grow into new stems (Fig. 4).

As *P. texense* has been purported to be a hybrid or not differentiated from *P. costatum*, it has not been included in keys to the genus. It clearly does not fit the description of any of the other species and this has lead to confusion when attempting to identify it. Of the 138 specimens identified as *P. texense* in the course of this study (not including the author's own collections), 22 were not initially identified to species or not identified as *Ptilimnium*, 34 were identified as *P. capillaceum*, 44 as *P. costatum*, 36 as *P. nuttallii*, and just two as *P. texense*. About one-third of these were annotated to *P. xtexense*, *P. capillaceum* ×*P. nuttallii*, or *P. costatum* by subsequent workers. This poor record of identification clearly demonstrates the need for a more inclusive and refined key. Previous keys to the genus have emphasized style length, number of segments of the involucral bracts, and whether the primary leaf segments are alternate or opposite on the rachis. Although these characters can be useful, there is variability and overlap among them and relying exclusively on these characters can lead to confusion. For this reason, additional characters have been utilized in the key below.

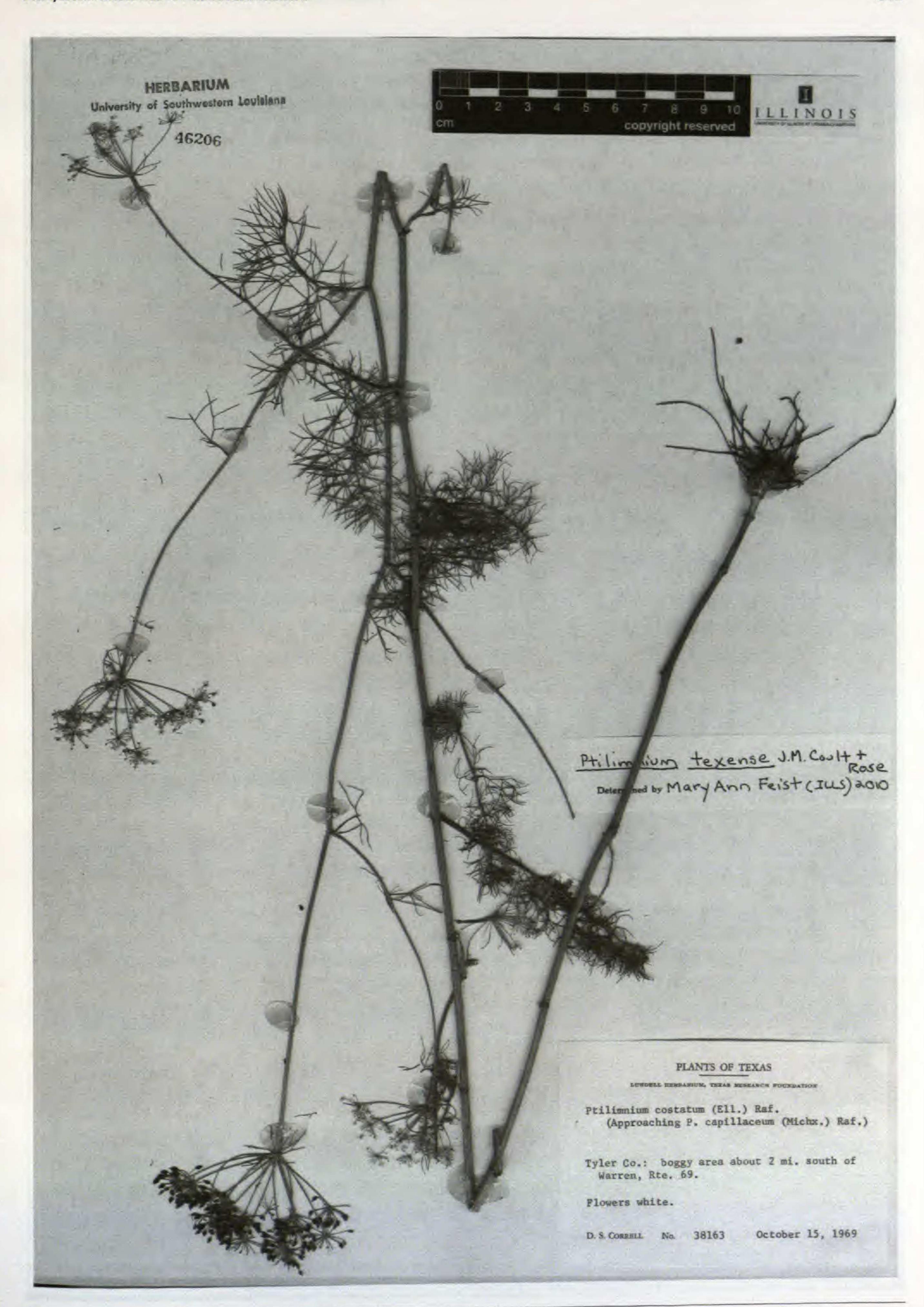


Fig. 2. Scanned image of Ptilimnium texense (LAF-46206) collected by D.S. Correll in 1969.

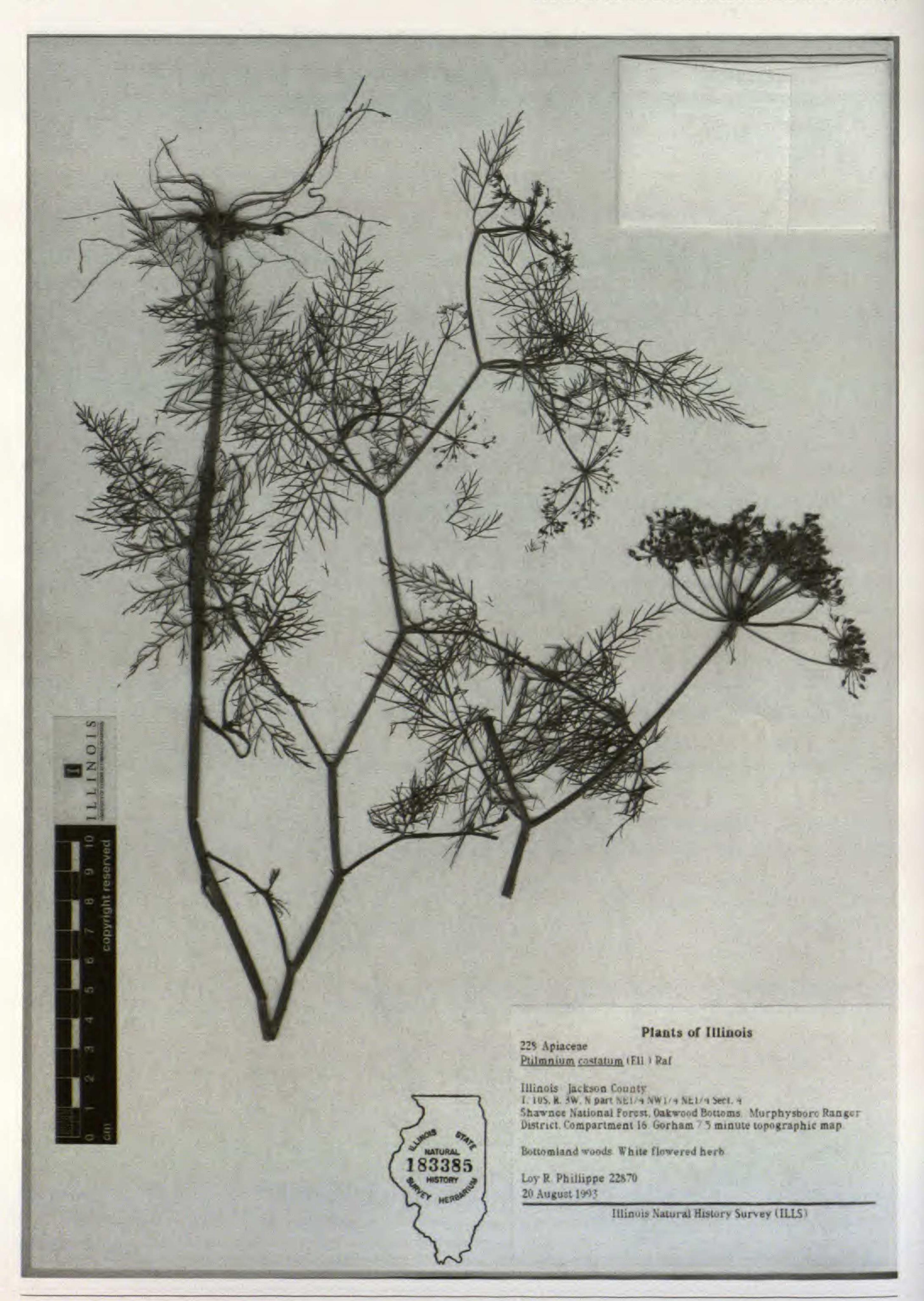


Fig. 3. Scanned image of Ptilimnium costatum (ILLS-183385) collected by L.R. Phillippe in 1993.



Fig. 4. Corms with root-budding of Ptilimnium costatum (top) and Ptilimnium texense (bottom).

KEY TO PTILIMNIUM

- Middle and upper petiole bases not papillate on the abaxial surface; styles (0.3–)0.4–2 mm long (on fruit), spreading to strongly recurved; calyx teeth > 0.2 mm, narrowly triangular.

P. nuttallii

- Mid-stem leaves with (6–)7–16 nodes along the rachis, primary leaf segments whorled or verticillate at the major nodes; individual leaf segments shorter than the rachis (rarely as long as in *P. texense*); involucral bract segments (1–)3(–7); stem thickened and rounded at the base forming a globose or slightly elongate corm; styles (0.3–)0.5–2 mm long; fruit 2.2–4 mm long, dorsal ribs narrow, sharp-edged to blunt; flowering Jul–Oct, fruiting mid-Jul–Nov.
 - 3. Leaf segments flat (at least near the nodes but usually throughout), midvein visible; mid-stem leaves with (8–)10–16 nodes per rachis, longest primary segments with 9–22 secondary segments; leaf shape in outline deltoid or trullate (trowel-shaped), leaf segments getting progressively and noticeably shorter towards apex, apex acute; styles (0.8–)1–2 mm long, slightly spreading to spreading; flowering Jul–Oct, fruiting mid-Jul–Oct; bottomland forest, swamps, streambanks, and pond margins

P. costatum

3. Leaf segments 3–4-angled to subterete, midvein not visible; mid-stem leaves with (6–)7–10 nodes per rachis, longest primary segments with 3–7(–8) secondary segments; leaf shape in outline oblong or oval, leaf segments not getting progressively and noticeably shorter towards apex, apex blunt; styles (0.3–)0.5–0.8(–1) mm long, spreading to strongly recurved; flowering Aug–Oct, fruiting Sep–Nov; seeps, bogs, and wet pine savannas

P. texense

TAXONOMIC DESCRIPTION

Ptilimnium texense J.M. Coult. & Rose, Contr. U.S. Natl. Herb. 12:445. 1909. Type: U.S.A. Texas. Harris Co.: near Hockley, Sep 1890, F.W. Thurow s.n. (HOLOTYPE: US).

Plants perennial, 5–12 dm, roots from a small rounded corm at base of stem. **Leaves**: blades 3–12 cm, stiff, 3-dimensional, oblong to oval in outline, apex blunt, mid-stem leaves with (6–)7–10 nodes along the rachis, 3–5 primary leaf segments at the major nodes; leaf segments dissected, filiform to linear, 3–4-angled to subterete, midvein not visible, individual leaf segments shorter than (–as long as) the rachis, primary leaf segments not getting progressively and noticeably shorter towards apex, longest primary segments with 3–7(–8) secondary segments; petioles 0.5–3 cm, hyaline borders narrow, often inconspicuous and only visible at the distal and proximal ends, abaxial surface not papillate at the base. **Peduncle** 2–12 cm. **Umbels** 3–8(–10), rays 8–20(–25), 1–3.5(–4.5) cm, subequal to of varying lengths; involucral bracts linear, entire or 3-parted, rarely further divided. **Pedicels** 2–12 mm. **Flowers** 12–24 per umbellet; calyx teeth conspicuous, 0.2–0.4 mm, narrowly triangular; petals (0.6–)0.7–1.3 mm; styles (0.3–)0.5–0.8 (–1) mm, spreading to strongly recurved. **Schizocarps** 2.2–3.5 × 1.5–2.2 mm, ovate to orbicular, slightly compressed laterally, often maroon- or purple-tinged, dorsal ribs narrow, blunt, corky-thickened extension of the lateral ribs conspicuous; oil tubes dark brown. Flowering/fruiting Aug–Oct/Sep–Nov.

APPENDIX 1

ARKANSAS. Calhoun Co.: 2 mi S of Harrel, clearcut sweetbay Magnolia woods, 17 Sep 1987, Sundell & Etheridge 7922 (BRIT, NO). Columbia Co.: Emerson, 8 Sep 1948, D.M. Moore 480649 (SMU, UARK).

LOUISIANA. Allen Pa.: off LA 112 ca. 4 mi W of Elizabeth, infrequent in pine forest, 5 Sep 1981, *C.M. Allen 11315* (LSU). **Beauregard Pa.:** beside LA 110 6.5 mi SE of Merryville near Bearhead Creek, wet area, 3 Aug 1974, *R.D. Thomas 40979* (TENN). **Calcasieu Pa.:** Lake Charles, prairies, 14 Sep 1906, *R.S. Cocks s.n.* (NO); 4 mi S of Holmwood, grassy roadside, 23 Sep 1967, *J.W.*

¹Ptilimnium ahlesii Weakley & Nesom (2004) is included under P. capillaceum in this key. Studies utilizing nrITS and cpDNA sequences found no molecular difference between these two taxa (Feist & Downie 2008; Feist & Downie unpublished data). The morphological distinctiveness of P. ahlesii is also questioned by the author and is currently under review.

Thieret 27955 (LAF); S of Lake Charles, on Hwy. 27, prairie, 19 Sep 1969, C.A. Brown 20872 (LSU). Grant Pa.: Breezy Hill vicinity, ca. 1 mi N, Kisatchie N.F., longleaf pine woods on silty soil in a hillside seepage bog, 18 Aug 1997, P.E. Hyatt & A. Martin 7691 (USCH). Jackson Pa.: beside LA 1472 mi NW of LA 34 at Winn Parish Line S of Chatham, swampy area, 7 Sep 1987, R.D. Thomas 101940 (TENN). Jefferson Davis Pa.: roadside ditch and RR ROW beside US 165 N of Fenton, 18 Oct 1975, R.D. Thomas 47944 (FLAS, USCH). Natchitoches Pa.: ca. 7.5 mi NE of Kisatchie, in seepage area with pitcher plants, 28 Sep 1974, C.M. Allen 5961 (LAF); near bridge on Longleaf Vista (FSR 337), ca. 9 mi NW of Gorum, abundant in bog, 28 Aug 1976, K. Vincent 561 (DUKE, GA, LAF); Red Dirt Game Management Area, Kisatchie N.F., near Montrose Rd., stream near bog, 16 Sep 1976, W.C. Holmes 2820 (UNA); on Strange Rd. in Kisatchie N.F., N of LA 479 and W of Goldonna near Ragan, bog, 17 Oct 1986, R.D. Thomas & N. Gilmore 98858 (MO); Strange Road Bog, 0.8-0.9 mi N on FR 570, off Hwy. 479 near Goldonna, Kisatchie N.F., pitcher plant bog, 22 Aug 1987, B.R. & M.H. MacRoberts 545 (LSUS); Strange Road Bog, 0.8-0.9 mi N on FR 570, off Hwy. 479 near Goldonna, Kisatchie N.F., pitcher plant bog, 20 June 1987, B.R. & M.H. MacRoberts 432 (LSU); beside USFS 380 (Middle Branch Rd.) 5 of Longleaf Vista Rd. in Kisatchie N.F., E of LA 117, 17 Sep 1988, R.D. Thomas 107272 (TENN); beside LA 479 at Strange Rd. W of Goldonna in Kisatchie N.F., moist seepage area, 14 Aug 1989, R.D. Thomas & D. Bell 112081 (ILL); Kisatchie N.F., Winn Dist., Compt. 18, along Strange Rd. (USFS 570) N of Pitcher Plant Bog and S of Luster Creek, N of LA 479 W of Goldonna, pitcher plant bog, 29 Aug 1997, R.D. Thomas 155187 (GA); Strange Road Bog, N of LA 479 and FSR 570 NW of Goldonna, pitcher plant bog area in pine forest, 26 Sep 2001, D.M. Ferguson 366 (LSU); ca. 0.1 mi N of SR 126 and 0.7 mi E of SR 1233 (Pine Ridge) and 0.1 mi N of SR 126, Kisatchie N.F., in bog opening with longleaf pine and pitcher plant, 24 Sep 2009, M.A. Feist & B. Molano-Flores 4426 (ILLS). Rapides Pa.: IPCO slash plantation (thinning study) near Hineston, longleaf pine, 20 Aug 1963, H.E. Grelan 340 (USFS); next to Pecan Rd., just N of Arrowhead Rd., weedy clearcut longleaf pine forest, 20 Aug 1993, C. Slaughter & J. Thompson 4115 (LSU); Hwy. 488 to FS 240, left at FS 2402, along dirt track, Kisatchie N.F., Evangeline District, bog with Rhexia petiolata, 15 Sep 1993, J. Bruser 229 (LSU); W of Brushy Creek Rd., 4.85 km SW of S end of West Twin Lake, ca. 7.1 km W of Flagon Bayou, wooded seep, 16 Oct 2003, P. Douglas, M. Arnett, & N. Hastings 1125 (LSU). Vernon Pa.: near Pickering, boggy branch long leaf pine hills with Magnolia glauca, black gum, poison sumac, pitcher plant, 3 Oct 1936, C.A. Brown 6878 (LSU); 2 mi S of Evans along highway to Merryville, roadside near creek, 14 Aug 1967, A. Lasseigne 730 (LAF); ca. 1.5 mi E of Pickering, roadside ditch, 4 Sep 1967, J.W. Thieret 27754 (LAF); 2 mi W of LA 464 and Caney, swampy area in pine barrens, 3 Oct 1967, R.D. Thomas 5515 (FLAS); Hwy. 312 near Toledo Bend Dam on Sabine River, long leaf pine woods, 4 Oct 1969, C.A. Brown 21067 (LSU); ca. 3.5 mi E of Rosepine, abundant in bog near pond, 25 Sep 1976, K. Vincent & C.M. Allen 655 (LAF, USF); along Pearl Creek ca. 3/4 mi NE of Burr Ferry on LA 111, infrequent in pine woods along Pearl Creek, 4 Nov 1979, K. Vincent & C.M. Allen 3220 (LAF); on LA 28 ca. 1.2 mi W of Rapides-Vernon Parish line, pitcher plant bog, 11 Sep 1981, F.M. Givens 2217 (LSU); W of Plainview Community Rd., 2.6 mi N of LA 392 and Hornsbeck, pitcher plant bog on gentle slope in pine woods, 13 Oct 1985, R.D. Thomas 94549 (MO, TENN); E of Drake's Creek, ca. 2 mi E of Johnsonville Church and LA 10, ca. 7 mi E of Pickering, Kisatchie N.F., 7 Sep 1987, R.D. Thomas 101487 (USCH); ca. 0.5 mi N of Big Branch Creek along Plainview Community Rd. 1.5 mi N from LA 392, 0.4 mi E of jct. LA 392 and US 171 in Hornbeck, sandy pasture and roadside with hillside seeps, 23 Aug 1989, L.E. Urbatsch 5977 (LSU); S of 421 near Yoke Creek, Kisatchie N.F., bog in clay-soiled seepage savanna, 14 Sep 1990, M.S. Olson 355 (LSU); Fort Polk Army Post, S of Range 8 and 8A, disturbed area in rolling upland, fine sandy loam, 27 Jul 1991, C.M. Allen & A. Allen PLK0541 (OKL); Cooter's Bog, Kisatchie N.F., longleaf pine savannah with pitcher plant bog, 25 Sep 2009, M.A. Feist & B. Molano-Flores 4447 (ILLS). Winn Pa.: 4 mi W of Winnfield, vicinity of limestone quarry, boggy open soil at edge of pocosin, 3 Aug 1938, D.S Correll & H.B. Correll 10042 (DUKE); ca. 2.5 mi N of Verda, locally abundant in bog in pine forest, 11 Aug 1976, K. Vincent & C.M. Allen 7152 (LAF, OS); ca. 1.1. mi E of SR 1233 (at Pine Ridge), just S of SR 126, Kisatchie N.F., roadside with Cephalanthus occidentalis, Oxypolis rigidior, Eryngium integrifolium, etc., 24 Sep 2009, M.A. Feist & B. Molano-Flores 4442 (ILLS).

TEXAS. Anderson Co.: Gus Engeling W.M.A., NW of Palestine, boggy area around Lake 2, 28 Sep 1980, C. Crozier s.n. (BAYLU); Gus Engeling W.M.A., NW of Palestine, Lake 2 bog area, pasture 2, boggy area, with Eupatorium, Helianthus, Eryngium, 16 Oct 1993, M. Dubrule Reed 1353 (TAMU); Gus Engeling W.M.A., NW of Palestine, Lake 2 bog area, pasture 2, sandy soil, with Eupatorium, Helianthus, Eryngium, 16 Oct 1993, M. Dubrule Reed 1354 (TAMU); Chester's Pitcher Plant Bog, N end of Gus Engeling W.M.A., on Gibson Branch, S of FM 2961 just downstream from lake, pitcher plant bog, 9 Aug 1997, B.R. & M.H. MacRoberts 3412 (BRIT, TEX). Angelina Co.: Angelina near Boykin Springs, Angelina N.F., seepage slope along stream in longleaf pine area, 30 Nov 1962, D.S. Correll 26860 (LL); 2 mi NW of Bouton Lake along road on way to Rte. 69, Angelina N.F., on open-wooded seepage slope, 30 Nov 1962, D.S. Correll 26883 (LL); about lake at Boykin Springs, Angelina N.F., wet soil, 7 Sep 1967, D.S. Correll 34925 (LL); SW of FSR 313 and FSR 313A, N of Boykin Spring Recreation Area, Angelina N.F., acid seep in old-growth, burned, dry upland longleaf pine savannah, 14 Aug 1989, S.L. Orzell & E.L. Bridges 11438 (TEX). Austin Co.: Austin Co., 15 Oct 1939, B.C. Tharp s.n. (MO, TEX). Brazos Co.: at College Station, road ditch, 25 Aug 1948, N.L. Byrd 230 (OSC). Cherokee Co.: Jacksonville, 8 Oct. 1884, J.F. Joor s.n. (MO). Freestone Co.: ca. 14.5 mi S of Fairfield, in bog, sandy valley bottom, 2 Oct 1949, L.H. Shinners 11830 (SMU); ca. 15 mi S of Fairfield on US 75, 20 Sep 1958, H. Gentry 2897 (BRIT, UNC); Womach Ranch, 7 mi NE of Buffalo, deep muck quaking bogs, upland basin (bowl), 17 Sep 2003, J. Singhurst & E. Bridges 12343 (BAYLU). Hardin Co.: Nona, damp flat pinebarrens, 15 Nov 1893, C. Mohrs.n. (US); cut over longleaf pine, 5 Sep 1924, B.C. Tharp 3158 (TEX); near Kountze, in sour flat in longleaf pine, 25 Aug 1945, S.R. Warner 47-12 (TEX); 4 mi W of Silsbee, savannah, 10 Oct 1965, D.S. Correll 31994 (LL, MO); along roadside of Hwy. 327 between Silsbee and Kountz, along pipeline crossing, 30 Sep 1971, P.A. Amerson 834 (SMU); Roy

E. Larson Sandylands Preserve, Tract 4, ca. 3.3 mi E of jct. of Hwy. 69 and Hwy. 418 on 418, S side of 418 and W side of Village Creek, 12 Aug 1994, J. Singhurst 2270 (BAYLU); Roy E. Larson Sandylands Preserve, Tract 4, ca. 3.3 mi E of jct. of Hwy. 69 and Hwy. 418 on 418, S side of 418 and W side of Village Creek, 15 Oct 1994, J. Singhurst 2019 (BAYLU); Roy E. Larson Sandylands Preserve, Tract 4, ca. 3.3 mi E of jct. of Hwy. 69 and Hwy. 418 on 418, S side of 418 and W side of Village Creek, 15 Oct 1994, J. Singhurst 2050 (BAYLU); roadside ditch just outside of Roy E. Larson Sandylands Preserve, within the Hyatt Lake Estates, roadside ditch near longleaf pine savannah, 25 Sep 2009, M.A. Feist & B. Molano-Flores 4464 (ILLS). Harris Co.: near Hockley, Sep 1890, F.W. Thurow s.n. (US). Henderson Co.: 8 mi from Athens, seepage slope along stream, 28 Aug 1946, V.L. Cory 14188 (LL). Houston Co.: Grapeland, open sandy bogs, 16 Sep 1918, E.J. Palmer 14423 (MO). Jasper Co.: off TX 63 NW of Beans Place, in pineland, 10 Sep 1942, C.L. & A.A. Lundell 11903 (LL); in longleaf pine region in rolling country, 6 mi N of Kirbyville, evergreen shrub bog, 10 Nov 1962, D.S. Correll 26755 (LL); 2 mi W of McGee Bend Dam, seepage slope among Magnolia virginiana and Sarracenia, 13 Nov 1963, D.S. Correll 28638 (LL); Boykin Bog, bog, 23 Aug 1964, R.P. Turner 144 (TEX); N side of Little Rocky Creek NE of Grubbs House, Little Rocky Preserve, ca. 3.4 mi E of jct. US 96 and FM 1007 near Browndell, locally frequent in wet sandy soil in forested seep in loblolly pine-hardwoods forest below open hillside seepage bog, 24 Sep 1997, W.R. Carr 17060 (TEX); E of CR 348A, along small roadside stream in cutover longleaf pine savannah, 25 Sep 2009, M.A. Feist & B. Molano-Flores 4458 (ILLS); E of CR 348A, along small stream in cutover longleaf pine savannah, 25 Sep 2009, M.A. Feist & B. Molano-Flores 4463 (ILLS). Jefferson Co.: Beaumont, 15 Sep 1936, J.L. Hooks s.n. (TEX). Leon Co.: ca. 8.5 mi NE of Buffalo on US 79, seepage Sarracenia bog, 16 Sep 1994, W.C. Holmes 7466 (BAYLU); Cripple Fawn Ranch, NE of Flynn, Sarracenia bog with Pluchea, Myrica, Lobelia, and Solidago, 10 Nov 1995, M. Dubrule Reed 1738 (TAMU). Nacogdoches Co.: near Nacogdoches, 24 Sep 1938, E. Whitehouse 11376 (SMU). Newton Co.: SF 1, 5 mi E of Kirbyville, moist sandy woods, 30 Sep 1945, V.L. Cory 49817 (SMU, US); 1.5 mi E of county line along Farm Rd. 363 to Bon Wier, savannah between road and railroad, 30 Oct 1968, D.S Correll & H.B. Correll 36692 (LL); 5 mi due W of Deweyville, edge of moist woods, 14 Sep 1968, D.S. Correll 36530 (LL); Scrappin Valley Distinctive Site, Temple Inland Corp Land, 5.1 mi N of jct. of R 255 and Hwy. 87 at Mayflower Community on Hwy. 87, E side of Hwy. 87, Sphagnum-beakrush community, hill-side seepage slope bogs, acid seep spring bogs, 15 Oct 2002, J. Singhurst 11262 (BAYLU). Robertson Co.: near Newbaden, widespread on bog, 30 Oct 1943, J.J. Brady, B.C. Tharp, & F.A. Barkley 13750 (DUKE, MO NO, OKL, OKLA, RM, TEX, UARK, UNC, US); 15 mi SE of New Baden, moist area of bog, 11 Oct 1948, E.M. Trew, Jr. 96 (TEX); 4 mi E of New Baden, bog, 21 Aug 1948, G.L. Webster & C.M. Rowell 1904 (TEX); 5 mi E of New Baden, peat bog, 24 Oct 1948, G.L. Webster & C.M. Rowell 1953 (TEX, UARK); Southworth bog, ca. 15 mi SE of New Baden, moist portion of bog, 11 Oct 1948, J.J. Sperry 2157 (TAMU); Southworth Peat Bog, 12 mi E of New Baden, bog in Carrizo sands with cattails, pitcher plants, and panic grass, 20 Aug 1954, E.L. Rabb 108 (TAMU); S.W. 1/4 Camp Creek Lake Quad., Mill Creek Bog, bog, 4 Oct 1981, T. Starbuck 1097 (BRIT, TAMU). Smith Co.: Swan, swamps, 17 Sep 1902, J. Reverehon 3193 (MO, US); Swan, swamps, 17 Sep 1902, J. Reverchon s.n. (MO, US); western Tyler, on ROW of Cotton Belt Railway, frequent in muddy ground along a small drainageway, 5 Sep 1949, V.L. Cory 56892 (US). Tyler Co.: Kirby Forest, near Warren and Kountze, 25 Aug 1945, S.R. Warner 475 (TEX); ca. 2 mi NE of Warren, in a draw near a creek, 1 Oct 1945, V.L. Cory 49869 (OKLA, SMU, US); 2.5 mi S of Warren, frequent in pitcher plant bog, 28 Sep 1948, V.L. Cory 54898 (LL, SMU); ca. 10 mi E of Hillister on road to Spurger, evergreen shrub bog, pinelands, 15 Nov 1963, D.S. Correll 28680 (LL); ca. 2 mi S of Warren on Rte. 69, boggy area, 15 Oct 1969, D.S. Correll 38163 (LAF, LL, MO, UNC); Turkey Creek Unit, Big Thicket National Preserve, longleaf pine-black gum savannah, 10 Sep 1981, A. Pecotte 32 (TAMU); NW corner of Big Thicket Bogs & Pineylands Preserve (TNC), 100 ft S of CR 4770, ca. 0.4-0.5 mi E of its jct. with US 69/287 near Lake Hyatt, frequent in moist to wet sandy loam in portion of boggy wetland with Sphagnum and Sarracenia, 25 Sep 1997, W.R. Carr 17084 (TEX). Wood Co.: in a bog below dam of a small lake, ca. 2 mi N of Mineola, Rte. 37, bog, 29 Sep 1967, D.S. Correll 35023 (LL). County unknown: damp flat pinebarrens, 15 Nov 1893, C.N. Sabain s.n. (US).

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